

Drought as an Inciting Mortality Factor in Scots Pine Stands of the Valais, Switzerland

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ABSTRACT

During the 20th century, high mortality rates of Scots pine (*Pinus silvestris* L.) have been observed over large areas in the Rhône valley (Valais, Switzerland) and in other dry valleys of the European Alps. In this study, we evaluated drought as a possible inciting factor of Scots pine decline in the Valais. Averaged tree-ring widths, standardized tree-ring series, and estimated annual mortality risks were related to a drought index. Correlations between drought indices and standardized tree-ring series from 11 sites showed a moderate association. Several drought years and drought periods could be detected since 1864 that coincided with decreased

growth. Although single, extreme drought years had generally a short-term, reversible effect on tree growth, multi-year drought initiated prolonged growth decreases that increased a tree's long-term risk of death. Tree death occurred generally several years or even decades after the drought. In conclusion, drought has a limiting effect on tree growth and acts as a bottleneck event in triggering Scots pine decline in the Valais.

Key words: drought; tree mortality; Scots pine (*Pinus silvestris* L.); air pollution; mortality risk; statistical models; tree rings; climate; competition.

INTRODUCTION

High Scots Pine Mortality in the Valais

Since the beginning of the 20th century, high Scots pine (*Pinus silvestris* L.) mortality rates have been observed at irregular intervals in the Rhône valley (Valais, Switzerland), one of the main valleys of the Central Alps (Figure 1) (Innes 1993; Rigling and Cherubini 1999). The decline of Scots pine in forests of the Valais is not a local phenomenon. High mortality rates of Scots pine have also been docu-

mented from other central alpine dry valleys of the European Alps, for example, from Austria (Inntal) and Italy (Valle d'Aosta, Vintschgau) (Vertui and Tagliaferro 1998; Rigling and others 1999).

The Scots pine decline in the Valais is distributed over a large area (approximately 5000 ha) between Martigny and Brig, with the highest occurrence until the 1980s in the areas of Charrat/Saxon, Pfywald (east of Chippis), and Visp (Flühler and others 1981; Kienast 1985b), and from the 1990s in the area from Salgesch (north-east of Chippis) to Brig (Figure 1). Within a site, declining or dead trees stand beside living, vigorous trees, resulting in a regular scatter of dead Scots pine trees. The causes for the deaths of these diffusely distributed trees are not obvious (Rigling and Cherubini 1999).

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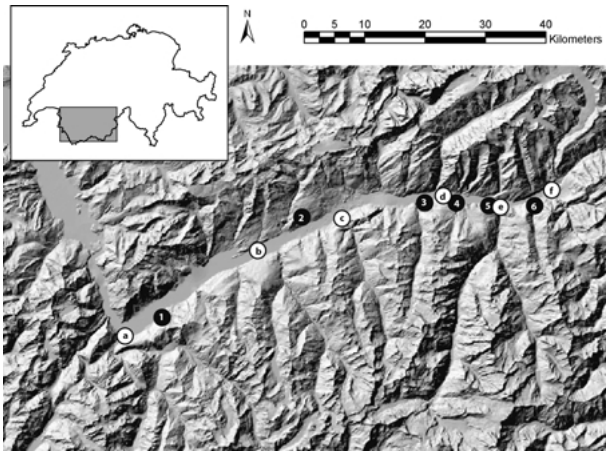


Figure 1. Map of the Rhône valley in the Valais, southwest of Switzerland, with study sites (numbers on black circles) and towns (letters on white circles). Study sites: 1 = Les Arbepins, Boutieu, Eponde, Creux du Dailley, Torrent des Croix, (Charrat/Saxon), 2 = LWF Lens, 3 = Turtmann, 4 = Raron, 5 = LWF Visp, 6 = Rohrberg Eyholz, Gliswald Gamsen. Towns: a = Martigny, b = Si-ion, c = Chippis, d = Steg, e = Visp, f = Brig. DHM25, reproduced by permission of swisstopo (BA035522).

Possible Causes of Scots Pine Decline

Between the 1920s and the early 1980s, scientific investigations on Scots pine decline in the Valais largely focused on fluorine emissions of nearby aluminum smelters that were built in 1907 in Martigny, 1908 in Chippis, and later, 1962 in Steg (Figure 1) (Faes 1921; Wille 1922; Bolay and Bovay 1965; Flühler 1981; Kontic and others 1986). Damage to Scots pine trees was shown to be greatest downwind (west–east) of pollution sources (Flühler 1983) and in the zone of atmospheric inversions (Kontic and others 1986). Scots pine is assumed to be one of the most sensitive conifers with regard to the impact of acid deposition and air pollutants (Bolay and Bovay 1965; Richardson and Rundel 1998).

After the installation of emission reduction technologies in aluminum smelters in the early 1980s, necrosis as a symptom of fluorine injury disappeared, and the mortality rates in the most severely affected areas decreased. However, mortality rates in the other areas remained high, or even increased in the 1990s in areas such as Visp, although the fluorine load has never been very high in this area (Rigling and Cherubini 1999; Rigling and others 1999).

The climate of the Valais suggests that drought could be an important cause of Scots pine decline (Flühler 1981; Kienast 1985b; Rigling and Cheru-

bini 1999; Rigling and others 2002). There is substantial evidence that drought stress promotes outbreaks of phytopathogens and secondary insects (Mattson and Haack 1987). Insect outbreaks often occur during or after unusually warm and dry weather, which decreases the resistance of stressed trees and provides favorable conditions for the population development of insects (Berryman 1989). In the Scots pine stands of the Valais, there is a latent presence of insects, including the common and lesser pine shoot beetle (*Tomicus piniperda* L., *T. minor*, Hart.), the pine processionary moth (*Thaumetopoea pityocampa*, Denis and Schiff.), the six-toothed bark beetle (*Ips sexdentatus*, Boern.), and the engraver beetle (*Ips acuminatus*, Gyll.) (Rigling and Cherubini 1999).

Besides pollutants, drought, phytopathogens and insects, stand aging and currently invading tree species may impose additional stress on the shade-intolerant Scots pine (Rigling and Cherubini 1999; Kienast and others 2004). Due to century-long management activities in the Valais, the extent of Scots pine forests has increased to 11% (12,000 ha) of the forested area, which is probably much higher than their natural abundance (Plumettaz Clot 1988). The shift in forest utilization after 1950 is one reason why many silver fir (*Abies alba*, Mill.), Norway spruce (*Picea abies* (L.), Karst.), and downy oak (*Quercus pubescens*, Willd.) trees and several shrub species currently are invading Scots pine stands (Rigling and Cherubini 1999; Rigling and others 1999; Kienast and others 2004).

Decline Disease Theory

It is not a single environmental factor, but rather a combination of multiple stress factors that likely causes the decline in Scots pine (Flühler 1981; Innes 1993; Rigling and Cherubini 1999). The decline disease theory, a general conceptual model for complex, stress-induced forest decline, provides a framework to relate tree death or the deterioration of a tree's vigor to a sequence of interchangeable environmental factors (Sinclair 1967; Manion 1981; Houston 1984). A three-step process of predisposing, inciting, and contributing factors that occur sequentially in time underlies the decline disease theory, as outlined briefly below.

Predisposing factors such as competition or air pollutants impact a tree during years or decades. These long-term factors are often expressed as reduced growth rates (Pedersen 1998b), and they increase a tree's susceptibility to short-term, inciting stresses, such as insect defoliation or drought. Such *inciting* factors affect the physiological func-

Table 1. Description of Study Sites

Data set	Site	Coordinates (N, E)	Altitude (m a.s.l.)	Aspect	Slope	Bedrock	Number of trees	Mean Tree Height (maximum)	Range
RGV	¹ Rohrberg Eyholz (6)	46°17'59", 7°56'49"	850	NNW	50%	Bündnerschiefer (schist)	59	10 (14)	1869–2000
	¹ Gliswald Gamsen (6)	46°17'49", 7°57'13"	950	NW	46%	Bündnerschiefer (schist)	58	10 (17)	1882–2001
	² LWF Visp (5)	46°17'52", 7°51'33"	680	N	80%	Bündnerschiefer (schist)	23	8 (12)	1912–2000
	³ Turtmann (3)	46°18'8", 7°43'7"	650	N	75%	Bündnerschiefer (schist)	32	– (–)	1817–1976
TR	³ Raron (4)	46°18'11", 7°47'24"	700	N	70%	Bündnerschiefer (schist)	16	– (–)	1874–1976
	⁴ Les Arbepins (1)	46°8'6", 7°9'50"	840	SW	27%	Calcareous sediments and schist	12	– (12)	1846–1979
CT	⁴ Boutieu (1)	46°8'4", 7°9'59"	880	NW	18%	Calcareous sediments	16	– (15)	1843–1979
	⁴ Eponde (1)	46°8'16", 7°10'41"	880	SW	27%	Calcareous schist	20	– (10)	1826–1979
	⁴ Creux du Dailley (1)	46°7'56", 7°11'14"	1240	SW	47%	Calcareous schist	15	– (13)	1746–1979
	⁴ Torrent des Croix (1)	46°7'19", 7°11'12"	1540	W	47%	Calcareous schist	13	– (15)	1833–1979
	⁵ LWF Lens (2)	46°16'14", 7°26'18"	1050	SE	90%	Limestone	20	11 (18)	1820–1997
L									

Data were collected by Bigler¹, Rigling², Schweingruber³, Kienast (1985a)⁴, Rigling and others (2003)⁵. Site, the numbers in parentheses correspond to the codes in Figure 1; Number of Trees, number of trees sampled; Mean Tree Height (Maximum), mean tree height and maximum tree height of sampled trees (where available) in meters; Range, range of years covered by crossdated trees.

tioning of a tree, and considerably reduce its vigor and potential for pathogen defense (Loehle 1988; Herms and Mattson 1992), resulting in rapid growth decline (Pedersen 1998a). Finally, a tree's fate often depends on the presence or absence of further, *contributing* stress factors that act over the short or long term. Examples are secondary, opportunistic insects, phytopathogens, mistletoe (*Viscum album* L.), or additional climatic events, which ultimately may kill stressed trees (Mattson and Haack 1987; Cherubini and others 2002).

Objectives and Research Questions

The objective of this study is to evaluate drought as a potential inciting factor of Scots pine decline in the Valais. Drought years are extracted from a long-term time series of a drought index. At 11 sites, three different methods are used to assess past tree responses to drought years: (i) the association between ring widths or standardized tree-ring indices and drought indices; (ii) the impact of drought on tree growth prior to death; and (iii) a method of computing a tree's annual mortality probability to estimate the relative mortality risk.

The following five questions are relevant for the present study: (1) To what extent do single drought years and multi-year drought periods affect tree growth? (2) How strong is the correlation between standardized tree-ring indices and drought indices? (3) What is the effect of drought on tree growth prior to death? (4) Is there a lag in the mortality response following a drought period? (5) How is the distribution of the mortality risk related to drought?

MATERIALS AND METHODS

Description of study sites and tree species

Eleven study sites were selected in the Rhône valley, an inner alpine valley in the Valais, Switzerland (Table 1, Figure 1). The valley is characterized by a dry-subcontinental climate with high insolation, low precipitation (between Visp and Sion, less than 600 mm precipitation per year), an annual mean temperature of about 9.5°C, and a pronounced wind system from west to east (Kienast 1985a; Lingg 1986).

The 11 sites were combined into five data sets, according to geographic location and altitude (Table 1, Figure 1): RGV (Rohrberg Eyholz, Gliswald Gamsen, LWF [Langfristige Waldökosystem-Forschung, Long-term Forest Ecosystem Research] Visp), TR (Turtmann, Raron), ABE (Les Arbepins,

Boutieu, Eponde), CT (Creux du Dailley, Torrent des Croix), L (LWF Lens). The bedrock at all sites belongs to the penninic, and all stands grow on relatively shallow Rendzic Leptosols (FAO soil classification system).

Scots pine (*Pinus silvestris* L.) is the dominant or one of the dominating tree species at all study sites. Scots pine, the most widely distributed species of all pines (Martínez-Vilalta and Piñol 2002), is a fast colonizing, light demanding pioneer tree, which establishes on wet as well as on dry sites, and grows on acid and also on calcareous soils (Ellenberg 1996; Rigling and Cherubini 1999). Scots pine is relatively resistant to frost and drought (Ellenberg 1996). Due to its low competitiveness, Scots pine is typically restricted to excessively wet, nutrient poor, or dry sites.

Drought Index

Climate data are from the Swiss Meteorological Institute (SMI) from the eastern climate station Visp (measurement period 1901–2001) and the western climate station Sion (1864–2001) (Figure 1). Both climate stations were moved in the 20th century and have incomplete measurement series for precipitation or temperature, thus, additional meteorological data of adjacent climate stations had to be used to bridge the missing climate series. For this purpose, monthly mean values and variances in the overlapping periods were adjusted to homogenize the data (O.U. Bräker, unpublished report).

A drought index (DRI; Eq. 1) was calculated using the formulation of Thornthwaite (1948), which requires monthly mean temperatures and precipitation sums:

$$\text{DRI} = P - \text{PET} \quad (1)$$

with P equal to the precipitation sum of August (previous year) to July (current year), and PET equal to the sum of estimated potential evapotranspiration of August (previous year) to July (current year) as a function of monthly mean temperatures and geographical latitude. This 12-month period was chosen because Rigling and others (2001) found that ring width of Scots pine on dry sites is more affected by water availability of the previous August than of the current August. The comparison of DRI with a more mechanistic drought index developed by Bugmann and Cramer (1998) showed no significant differences, thus suggesting that the use of a simple drought index (Eq. 1) is justified in our regional investigation. Values of DRI below zero indicate moisture deficits.

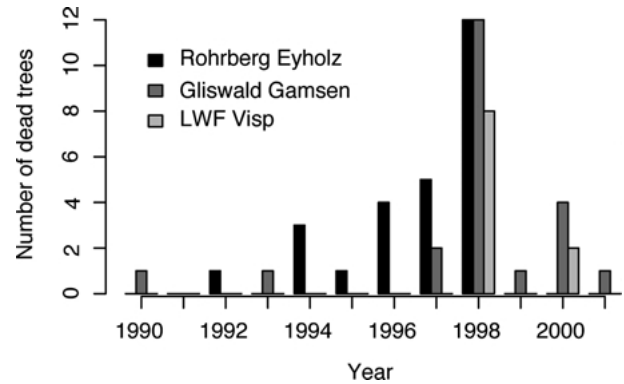


Figure 2. Annual mortality rates from the RGV sites (Rohrberg Eyholz, Gliswald Gamsen, LWF Visp). Only crossdated dead trees were considered.

The drought index from Visp was used to analyze data from the sites RGV and TR, which are located in the east of the Valais, and the drought index from Sion was used in combination with the more westerly sites ABE, CT, and L (see Figure 1 and Table 1).

Sampling of Trees and Processing of Tree-ring Series

Scots pine trees at the RGV sites were sampled in 2001 ($n = 140$; Table 1). At each site, standing dead and living trees of greater than 10 cm DBH (diameter at breast height) were selected in pairs for sampling. The living trees were selected that had similar DBH, competition, and microsite conditions as the dead trees (compare Bigler and Bugmann 2003). Two cores were taken at breast height (1.3 m) from each tree.

Tree rings were measured using a Lintab 3 measuring system (F. Rinn S.A., Heidelberg, Germany) and the TSAP tree-ring program (Rinn 1996). Two cores from each tree were crossdated and averaged (Fritts 1976). However, two trees from Gliswald Gamsen and one tree from both Rohrberg Eyholz and LWF Visp were excluded from further analyses because of decayed wood. In total, 124 trees could be crossdated. Fifty-five percent (32 of 58 trees) of the dead trees from RGV died in 1998 (Figure 2).

The tree-ring data of TR ($n = 48$), ABE ($n = 48$), CT ($n = 28$), and L ($n = 20$) were available from the dendrochronological database at WSL (Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf, Switzerland). These Scots pine trees had been sampled in 1977 (TR), 1980 (ABE, CT), and 1998 (L). When two cores per tree were available, the ring widths were averaged. All

data sets except for L contained a few dead trees, in which the last tree ring occurred prior to the year of sampling. However, the exact number of dead trees in these data sets could not be reconstructed, because a couple of trees might have died in the year of sampling.

The ring widths of the crossdated and averaged tree-ring series of all five data sets were converted to BAI (basal area increments; cm^2/y) and standardized into site-specific tree-ring chronologies. For standardization of each individual ring-width series, the observed values were divided by the expected values to remove the non-climatic low-frequency variability that is due to tree aging and stand dynamics (Fritts 1976). The ARSTAN software (Cook and Holmes 1984) was used to calculate expected values, and a double-detrending standardization was applied (Cook and others 1990). Tree-ring indices were estimated by sequentially fitting a negative exponential or linear function, followed by fitting a cubic smoothing spline (with 50% variance reduction using a 128-y spline) to the tree-ring indices to remove any residual growth trend. Finally, the individual series of each tree-ring indices were averaged using a biweight robust mean within each of the five combined data sets for a site-specific mean series of tree-ring indices.

Derivation of the Relative Mortality Risk

The method developed by Bigler and Bugmann (2004) was used to calculate a tree's annual mortality probability through time. It was adopted here to derive an estimator of the population-level mortality risk. The entire growth curves of the data set RGV ($n = 70$ dead trees, $n = 70$ living trees) were used for a total of $n = 9,254$ single tree rings to fit a logistic mortality model, based on the growth patterns of individual tree-ring curves:

$$\Pr(Y_{i,t}|X_{i,t}) = \frac{1}{1 + \exp [11.415 + 0.816 \times \text{locreg}_{5,i,t} + 1.456 \times \log(\text{relbai}_{i,t})]^{-1}} \quad (2)$$

where $\Pr(Y_{i,t}|X_{i,t})$ is the survival probability of tree i at time t , given the independent variables \mathbf{X} . Locreg_5 is the slope of a local linear regression calculated over 5 years of BAI, and the relative growth rate $\log(\text{relbai})$ is the log-transformed ratio of BAI and BA (basal area) (compare Bigler and Bugmann 2004). To take the autocorrelation of the dependent variable into account, an infinitesimal jackknife variance estimator (Lumley and Heagerty 1999) was applied to correct the biased variances.

All regression coefficients were highly significant ($P < 0.0001$).

The mortality model was applied to each of the crossdated trees of all five data sets (RGV, $n = 124$; TR, $n = 48$; ABE, $n = 48$; CT, $n = 28$; L, $n = 20$), resulting in individual probability curves of survival (compare Bigler and Bugmann 2004). For each calendar year, the percentage of trees with an increased mortality risk was estimated. This was achieved by estimating the percentage of trees with a survival probability below a threshold of 0.975 (Bigler and Bugmann 2004). Although decreasing (increasing) the threshold resulted in reducing (amplifying) the signal of the mortality risk, it did not strongly affect the overall pattern. Therefore, the precise choice of the threshold was not critical for this application. However, because some trees in the population may have died, but were not considered in the sample, the computed annual mortality risk is only valid for the sampled trees and has to be considered as a relative mortality risk.

RESULTS

Association Between Drought and Tree Growth

In the Visp area, single drought years such as 1921, 1933, 1944, 1947, 1974, and 1998 considerably decreased tree-ring indices in the short term (Figure 3A); this was however more pronounced for the RGV sites than for the TR sites. Persistent periods of moisture deficits had long-term negative effects on ring widths, for example, 1943–1950, 1956–1974, and 1996–2000 (Figure 4A).

In the Sion area, the negative impact of extreme drought on ring-width indices is evident for the years 1865, 1870, 1874, 1893, 1894, 1921, 1944, and 1976 (Figure 3B). Similarly, as in the case of Visp, series of drought years had a more sustained

effect on tree growth than single drought years, as shown by the periods 1880–1887, 1899–1909, and 1942–1950 (Figure 4B).

The non-parametric Spearman rank correlations R_s (Zar 1999) between the overlapping periods of ring-width indices and DRI (compare Figure 3), calculated with the statistical software "R" (version 1.5; R Development Core Team 2003), indicate a moderate association using all data (Table 2). For all five data sets, there was consistently a higher

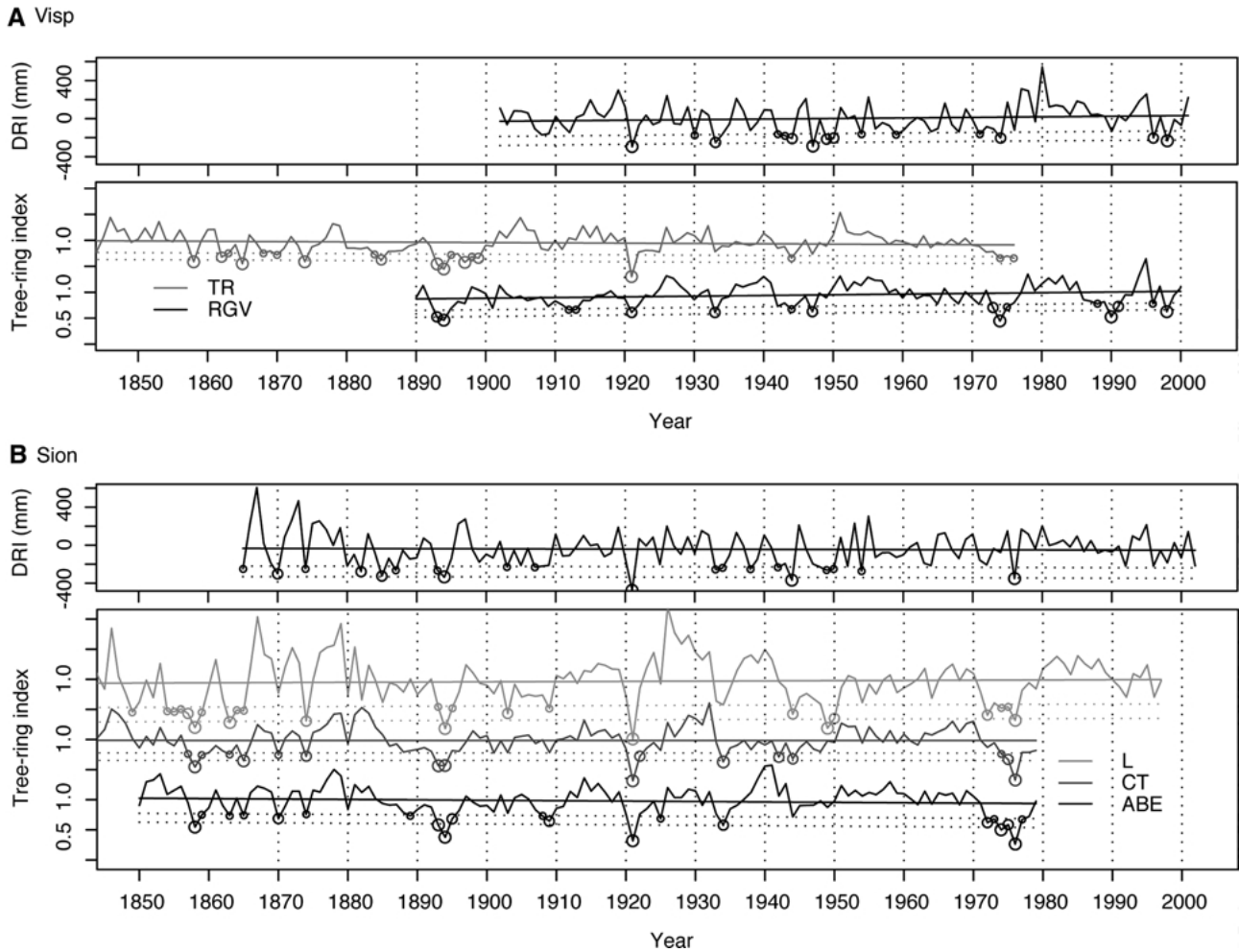


Figure 3. Comparison of drought indices (DRI) and standardized tree-ring indices for **(A)** Visp (RGV and TR sites), and **(B)** Sion (ABE, CT, and L sites). Lines indicate linear regressions, dotted lines indicate the lower 5 and 15% confidence limits (Zar 1999). Circles specify the intensity of drought years (5% *big circles*; 10% *medium circles*; 15% *small circles*). Only tree-ring indices of crossdated trees ($n \geq 5$ trees) are shown.

association between below-average drought indices and ring-width indices (Table 2) than between above-average drought indices and ring-width indices (Table 2). The statistical significance of the correlation coefficients was not calculated because the ring-width indices were autocorrelated up to a lag of 3–4 years.

Impact of Drought on Tree Growth Prior to Death

At the three sites comprising RGV, the averaged growth curves of dead and living trees decreased between 1951 and 1974, between 1978 and 1990, and after 1995 (Figure 5). The decreasing growth curves coincided with moisture deficits (1956–1974, 1996–2000) and with decreasing moisture availability (1980–1990). At the Rohrberg Eyholz

site, the growth curves of dead trees declined after 1976, whereas the growth of the living trees remained at a higher level (Figure 5A). Eighty-one percent (21 of 26 trees) of the dead trees died between 1996 and 1998, during or shortly after the single drought years of 1996 and 1998 (see Figure 2). At the Gliswald Gamsen site, the growth curves of dead and living trees started deviating from each other after 1990 (Figure 5B). At this site, 64% (14 of 22 trees) of the dead trees died between 1996 and 1998 (see Figure 2). At the LWF Visp site, dead trees showed a higher growth increase than the living trees between 1974 and 1998, but the growth curves again approached each other during the drought years of 1996 and 1998 (Figure 5C). The average growth of the living trees decreased from 1.26 mm in 1995 to 0.40 mm in 1998, while in the same period the growth of the dead trees was

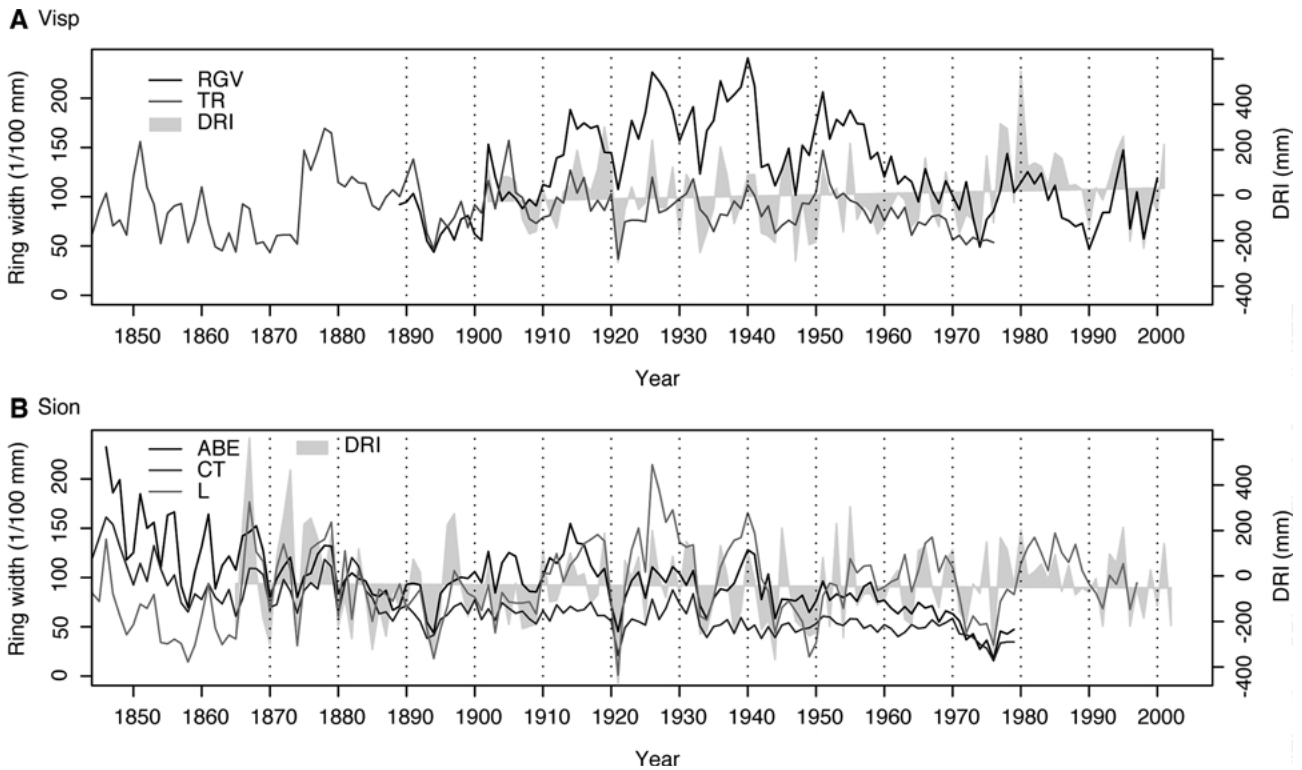


Figure 4. Drought indices (DRI) and averaged ring widths for (A) Visp (RGV and TR sites), and (B) Sion (ABE, CT, and L sites). The shaded areas show the values above and below the fitted regression lines. Only averaged ring widths of crossdated trees ($n \geq 5$ trees) are shown.

reduced from 2.20 to 0.45 mm. Eight of the ten dead trees died in 1998 (see Figure 2).

Distribution of the Relative Mortality Risk

The impact of moisture availability on the temporal distribution of the estimated relative mortality risk is given in Figure 6. For the RGV sites, an increased number of trees were subject to a high risk of dying in the years 1973–1976, 1987–1993, and 1996–2000 (Figure 6A). The first of these three risk periods occurred after the drought period 1971–1974, whereas the last period was caused by the moisture deficit of 1996–2000. The decreasing moisture availability from 1980–1990 coincided with increased mortality risk between 1987 and 1993. The trees at the two sites further west (TR) suffered mainly in 1921, corresponding to the very strong drought year (Figure 6B). Less accentuated were the late 1940s and 1972–1976; still, both periods of increased mortality risk coincide with a series of drought years. At the ABE sites, 1921, 1944, and particularly 1972–1978 reflect years with a relatively high number of stressed trees (Figure 6C). Strong drought coincides with the first two stress

Table 2. Spearman Rank Correlations between Drought Indices and Ring-width Indices

	Data set	R_s
(a) All Data	RGV	0.46 (100)
	TR	0.49 (75)
	ABE	0.43 (115)
	CT	0.42 (115)
	L	0.61 (133)
(b) Below Average	RGV	0.57 (51)
	TR	0.25 (40)
	ABE	0.39 (61)
	CT	0.45 (61)
	L	0.66 (70)
(c) Above Average	RGV	0.40 (49)
	TR	0.08 (35)
	ABE	0.17 (54)
	CT	0.14 (54)
	L	0.20 (63)

Shown are the correlation coefficients (R_s) for the overlapping periods (number of measurements in parentheses). The correlation coefficients were calculated (a) for all data, (b) for drought indices below the average, and (c) for drought indices above the average.

years only. The trees at the high-elevation CT sites experienced stress in the years 1858, 1893/1894,

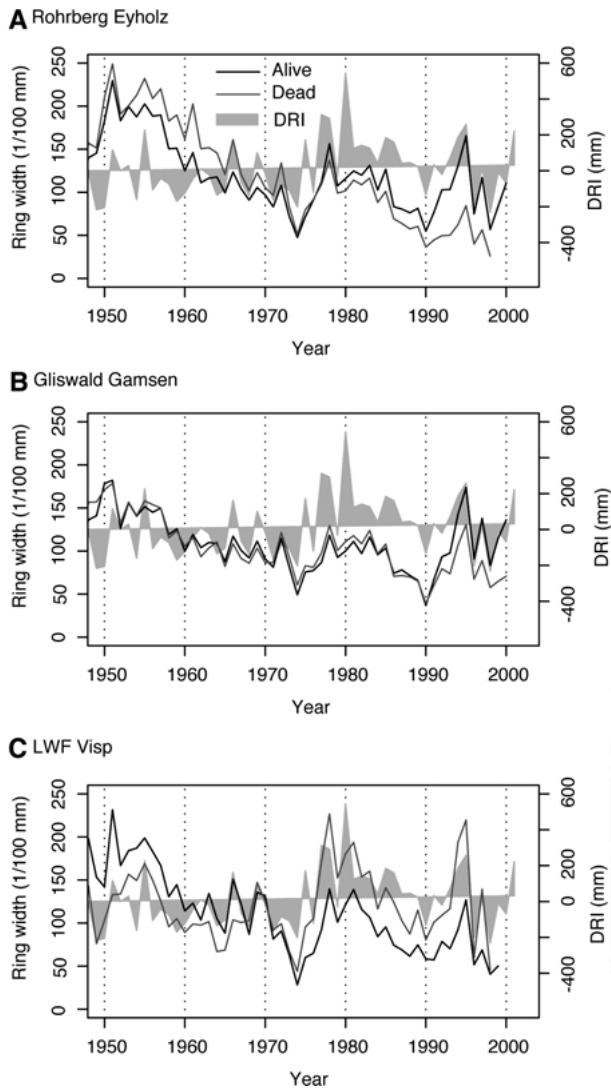


Figure 5. Averaged ring widths of dead and living trees (black lines living trees; gray lines dead trees) and DRI (shaded areas) for (A) Rohrberg Eyholz ($n = 26$ dead trees, $n = 29$ living trees), (B) Gliswald Gamsen ($n = 22$ dead trees, $n = 26$ living trees), and (C) LWF Visp ($n = 10$ dead trees, $n = 11$ living trees). Only averaged ring widths of crossdated trees ($n \geq 5$ trees) are shown.

1921, 1934, less pronounced in the 1940s, and strongly between 1971 and 1979 (Figure 6D). For the L site, the years 1858, 1874, 1894, 1921, 1944/1945, 1949/1950, 1972–1976, and 1992 were identified as stress years, and most of them were related to the occurrence of drought (Figure 6E).

DISCUSSION

Drought can exert a major influence on vegetation structure and species composition in a variety of ecosystems, such as grasslands (Clark and others 2002), tropical forests (Condit and others 1995;

Aiba and Kitayama 2002), and temperate forests (Clinton and others 1993; Elliott and Swank 1994; Jenkins and Pallardy 1995; Orwig and Abrams 1997; Villalba and Veblen 1998; Ogle and others 2000). The results presented in this study suggest that drought has a limiting effect on tree growth and acts as a bottleneck event in triggering Scots pine decline in the Valais. However, other factors besides the direct climate impacts would also need to be considered to better understand short- to long-term periods of low growth and the related mortality response. The role of drought as a stress factor as well as competition and insect occurrences are discussed in the context of the decline disease theory.

Drought as an Inciting Mortality Factor

Although drought-adapted, Scots pine trees in the arid climate of the Valais often approach their limit of hydraulic capacity, and therefore may react sensitively to drought, particularly on dry, shallow soils (Flühler 1981; Kienast 1985a; see also Hill 1993; Oberhuber 2001). The Scots pine trees in the Valais grow at their southern-most range (Rutherford and Webster 1987), which renders them particularly useful to study drought effects.

Recently, Martínez-Vilalta and Piñol (2002) have compared three pine species in north-eastern Spain in terms of their physiological reaction to drought. Only Scots pine stands were affected by drought-induced mortality, and the hydraulic conductivity per unit of leaf area was shown to be lowest for the most strongly affected population. Generally, pine species seem to be more vulnerable to xylem embolism than other conifers (Piñol and Sala 2000; Martínez-Vilalta and Piñol 2002; Martínez-Vilalta and others 2004; but see Irvine and others 1998). The absence of Scots pine decline outside of the main wind trajectories in the Valais (Flühler 1983) indicates that wind likely acts as an additional desiccating factor, which may intensify the effects of drought (Telewski 1995; Ennos 1997).

Drought indices and ring-width indices of the combined Scots pine data sets are moderately correlated ($R_s = 0.42$ – 0.61) (Table 2). For all five data sets, there were higher correlation coefficients between below-average drought indices compared to above-average drought indices (see also Fritts 1976). This indicates that during periods of moisture surplus, factors other than moisture availability affect tree growth, such as early or late frosts that occur frequently in the Valais due to the high terrestrial radiation (Lingg 1986).

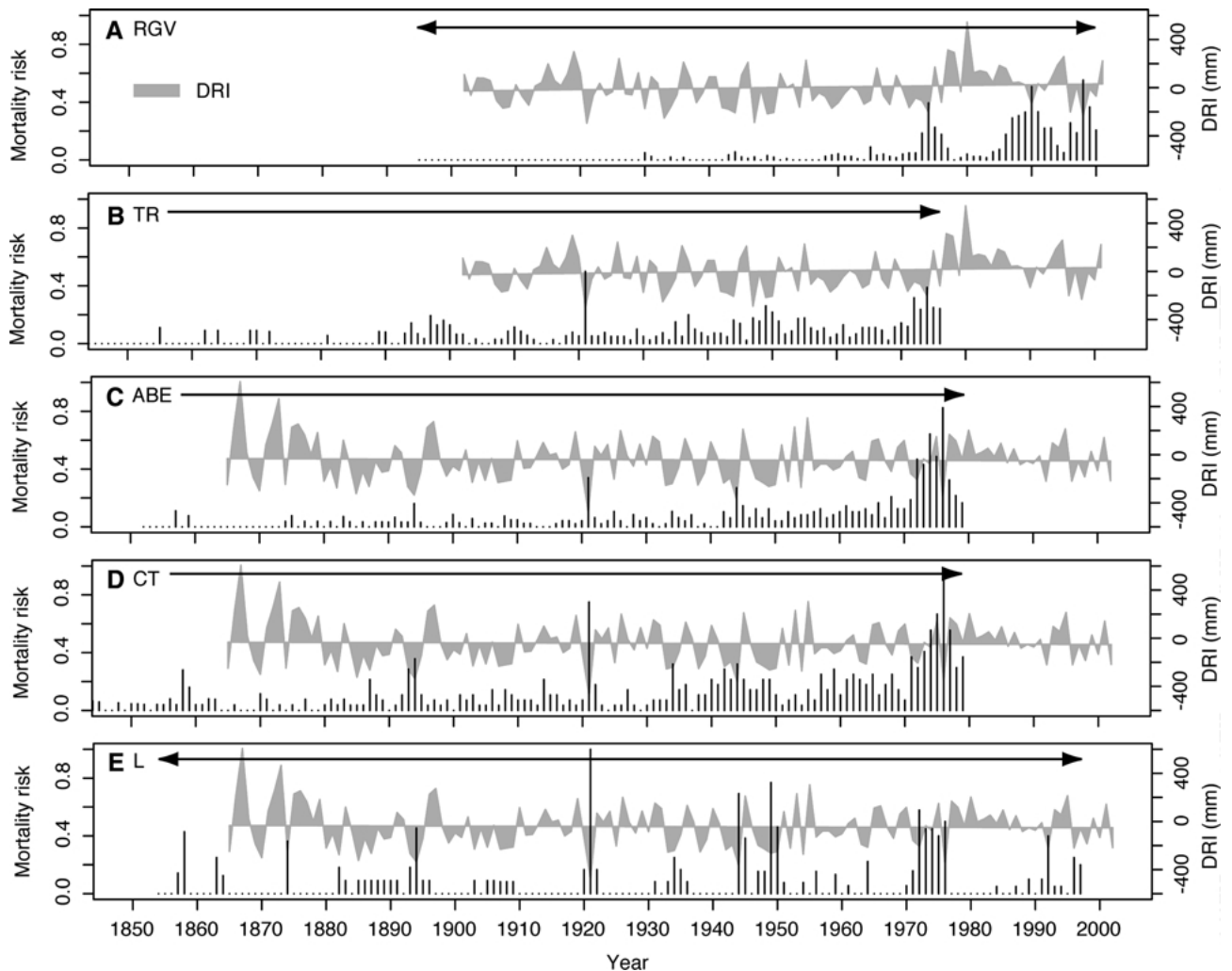


Figure 6. Annual relative mortality risks and DRI (*shaded areas*) of the five combined data sets RGV, TR, ABE, CT, and L. The *arrows* indicate the periods for which the mortality risks were calculated. Only mortality risks of crossdated trees ($n \geq 5$ trees) are shown.

In the short term, single drought years reduced tree growth in the investigated Scots pine stands during the year of drought (Figure 3), whereas multi-year periods of drought often initiated prolonged growth declines (Figures 4 and 5). The mortality model indicates years or periods of low growth often have an increased mortality risk, particularly with increased tree size (Figure 6; compare Eq. 2). In the context of the decline disease theory, it is noteworthy that very extreme drought years such as 1921, 1944, or 1974/1976 had a less sustained negative effect on tree growth compared to the series of medium drought years such as those during the 1940s for Visp and Sion, and 1956–1974 for Visp (Figures 3 and 4; compare Kienast and others 1981). Because trees at the RGV sites showed relatively high growth rates between

1910 and 1960 (Figure 4A), their modelled mortality risk was very low in this period (Figure 6A), even during the extreme drought year of 1921. The drought from 1956–1974 reduced tree vigor sustainably, resulting in long-lasting effects of relatively low growth rates even during the following period of moisture surplus (Figure 5).

Generally, extreme events such as drought tend to be crucial in initiating changes in forest ecosystems, much more than average climatic conditions (Oliver and Larson 1996; Innes 1998). The negative impact of single drought years on tree growth or the onset of declining growth prior to death has been observed for a wide range of tree species (Elliott and Swank 1994; Orwig and Abrams 1997; Pedersen 1998b; Villalba and Veblen 1998; Ogle and others 2000). However, the significance of

multi-year droughts having much more adverse and decisive effects on tree growth than single-year droughts has been emphasized only by a few studies (Stringer and others 1989; Biocca and others 1993; Jenkins and Pallardy 1995; LeBlanc 1998), and their findings are supported by the present study.

Differences Between Standardized Ring Widths and Modelled Mortality Risks

Despite the generally good agreement between the standardized ring widths and the relative mortality risk, some discrepancies are striking, which point to the fundamental difference between the two approaches. For example, the standardized ring widths identify the periods 1893–1895 and 1973–1976 as approximately equally stressful for all five data sets (Figure 3). The mortality model, however, mainly identifies the 1970s as a period of increased stress, and suggests that the trees had low to no risk of dying in the 1890s (Figure 6). Generally, standardized tree-ring indices reflect a mean growth response of stressed and non-stressed trees considering the relative vigor of the trees. The mortality model, however, returns the percentage of stressed trees in a sample taking into account the absolute vigor of individual trees.

Two reasons may have caused the increased mortality risk across sites (Figure 6): (1) the inclusion of tree size (BA) in the mortality model renders larger trees more likely to die than smaller trees (Bigler and Bugmann 2004; Bigler and others 2004); and (2) trees that died several decades ago were not included in the sample. For instance, many trees died between 1996 and 2000 at the RGV sites (Figure 2), which is also reflected by increased mortality risk (Figure 6A). Furthermore, L was the only data set that did not contain dead trees, and the modelled mortality risks were relatively low after 1976 (Figure 6E). The variability of BAI might also have resulted in increased mortality risk. However, we did not explicitly use BAI in the mortality model, but rather variables derived from BAI (see Eq. 2), which were robust in terms of changing variability of BAI.

Reasons for Growth Decreases During Drought

What might be the reasons for the prolonged growth decreases of Scots pine during multi-year drought? In a retrospective study on needle retention of Scots pines felled in 1996, Pouttu and Dobbertin (2000) found in the Visp region several periods with reduced needle amounts and in-

creased needle loss. These periods often coincided with the end of drought periods (that is, 1946–1949, 1973–1976, and 1990–1992). Drought leads not only to increased needle loss (Rebetez and Dobbertin 2004), but also to reduced needle and shoot length with fewer needle pairs in the following year (Clements 1969). This explains why the foliage amount is reduced over several years during and following a drought. As foliage amount affects both tree growth (Solberg 1999) and tree mortality (Dobbertin and Brang 2001), longer lasting effects of multi-year drought on growth and mortality can be expected.

Increasing growth rates after extreme drought years (Figures 3, 4, and 5) might be explained by release effects due to a relaxation of competition, since it is likely that a certain fraction of the trees in these stands died during or after the drought years (compare Orwig and Abrams 1997; Villalba and Veblen 1998; Martínez-Vilalta and Piñol 2002).

Lagged Mortality Response after Drought

The question of whether there is a direct link between climatic variability, particularly drought, and tree mortality rates has been addressed by other studies, supplying evidence of a strong association between extreme single drought years and tree mortality (Clinton and others 1993; Condit and others 1995; Villalba and Veblen 1998). However, if the mortality response does not occur immediately in the year of stress or within a lag of 1 year or 2 years, the association between environmental stress and tree mortality is likely to be weak and difficult to elucidate (Clinton and others 1993; Pedersen 1999). At the RGV sites in the Valais, drought periods (1956–1974, 1996–2000) or decreasing moisture availability (1980–1990) preceded the mortality response by several years or decades and were likely one of the major mortality factors (Figure 5). Although tree rings generally decline with time (Fritts 1976), we decided to use raw ring widths (Figure 5), because the averaged tree-ring series from the RGV sites showed no long-term declining trend (Figure 4A). In addition, we wanted to show, when growth declines started relative to previous growth rates, and when growth curves of dead and living trees started deviating, which would have not been feasible with standardized tree rings.

The agreement between the reconstructed relative mortality rates at the RGV sites and drought in the period after 1990 (Figures 2 and 5) does not necessarily imply a simple cause-effect relationship. Rather, the droughts in 1996 and 1998 can be

considered as additional contributing mortality factors (Figure 5). A lagged mortality response up to several decades following a severe drought has also been detected by Tainter and others (1984), Pedersen (1998b), and Jenkins and Pallardy (1995). These studies support our findings of lagged mortality responses after persistent drought periods, where further stresses may ultimately kill previously stressed trees.

Additional Predisposing and Contributing Mortality Factors

Increasingly dense stands due to the successional shift to more shade-tolerant species (Kienast and others 2004; Rigling and others 2004) may have imposed a further stress on the light demanding Scots pine trees. Competition acts as a long-term *predisposing* mortality factor (Peet and Christensen 1987; Bigler and Bugmann 2003).

Scots pine trees that are stressed by competition and drought eventually die because of additional *contributing* mortality factors, such as mistletoes (Dobbertin and others 2005), phytopathogens, additional drought, or insects (Rigling and Cherubini 1999). The century-long human influence on the forests of the Valais has resulted in an overrepresentation of Scots pine in comparison to its potential natural distribution (Plumettaz Clot 1988). This relatively high abundance may have contributed to the increased likelihood of insect epidemics in the 20th century, because insect populations can propagate more easily from one stand to another than between isolated stands (compare Berryman 1982). Furthermore, the significantly rising temperatures since about 1980 (Rebetez and Dobbertin 2004) are likely to have favored insect development rates and increased their populations in the Valais (Bale and others 2002). Because Scots pine is a host for a large number of potentially harmful insect species, the risk of insect outbreaks is high, especially after drought periods (compare de Groot and Turgeon 1998). As a consequence of severe water stress, Scots pine reduces the length of the induced defense reaction and lowers the resin content (Croisé and Lieutier 1993), which facilitates insect infestations in the affected stands (Mattson and Haack 1987; Cobb and others 1997; Czokajlo and others 1997).

CONCLUSIONS

The widespread occurrence of high Scots pine mortality in the Valais and in several other central alpine dry valleys of the European Alps suggests

that this phenomenon is caused by regional-scale factors and not by local anomalies. A multitude of biotic and abiotic stress factors, some of which have changed in the course of time, are currently assumed to be involved in the decline of Scots pine.

The shade-intolerance of Scots pine, a pioneer tree, renders this species more vulnerable to competition than some of the currently spreading tree species in the Valais, such as silver fir, Norway spruce, and downy oak. We presume that competition, which acts in the long term, predisposes Scots pine trees to die in the Valais.

We have presented evidence for the limiting effect of drought on tree growth and for the impact on mortality. Our results suggest that single, strong drought years have a short-term, reversible effect on tree growth, but there is no strong evidence that single drought years act as an inciting factor for tree mortality. However, we showed that multi-year drought reduces tree growth for several years or decades, thus increasing a tree's risk of death. Increased growth after drought periods is probably caused by release effects following drought-induced mortality of neighbor trees. Lagged mortality responses several years or decades after drought events complicate the analysis of cause-effect relationships.

Environmental factors such as competition and previous extended drought periods may impair Scots pine trees in the long term and make them more vulnerable to subsequent contributing factors such as drought, insects, mistletoes, or phytopathogens. We suggest that further investigations should focus on detailed analyses of tree-insect and tree-phytopathogen interactions on the individual tree and at the stand level. In addition, examining competitive relationships between Scots pine and other main tree species will provide a better foundation for understanding past and future dynamics of Scots pine forests.

In the Valais, the decline of Scots pine and the succession to shade-tolerant species will transform the Scots pine forests at lower elevations into downy oak-mixed deciduous forests (Kienast and others 2004; Rigling and others 2004) and at higher elevations into spruce-fir forests (Lingg 1986). This successional shift may also have implications in terms of plant biodiversity, because the current open-canopy pine forests are hot spots of species diversity.

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